Early above- and below-ground responses of subboreal conifer seedlings to various levels of deciduous canopy removal

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Abstract: We examined the growth of understory conifers, following partial or complete deciduous canopy removal, in a field study established in two regions in Canada. In central British Columbia, we studied the responses of three species (*Pseudotsuga menziesii* var. glauca (Beissn.) Franco, *Picea glauca* (Moench) Voss × *Picea engelmannii* Parry ex Engelm., and *Abies lasiocarpa* (Hook.) Nutt.), and in northwestern Quebec, we studied one species (*Abies balsamea* (L.) Mill.). Stem and root diameter and height growth were measured 5 years before and 3 years after harvesting. Both root and stem diameter growth increased sharply following release but seedlings showed greater root growth, suggesting that in the short term, improvement in soil resource capture and transport, and presumably stability, may be more important than an increase in stem diameter and height growth. Response was strongly size dependent, which appears to reflect greater demand for soil resources as well as higher light levels and greater tree vigour before release for taller individuals. Growth ratios could not explain the faster response generally attributed to true fir species or the unusual swift response of spruces. Good prerelease vigour of spruces, presumably favoured by deciduous canopies, could explain their rapid response to release.

Résumé : La croissance de conifères établis sous un couvert de feuillus a été étudiée suite à différentes intensités de coupe dans deux régions au Canada. Dans le centre de la Colombie-Britannique, les auteurs ont étudié les réactions de trois espèces (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco, *Picea glauca* (Moench) Voss × *Picea engelmannii* Parry ex Engelm. et *Abies lasiocarpa* (Hook.) Nutt.) alors que dans le nord-ouest du Québec, ils ont étudié une seule espèce (*Abies balsamea* (L.) Mill.). La croissance en diamètre de la tige et des racines et la croissance en hauteur ont été mesurées 5 ans avant et 3 ans après la coupe. La croissance en diamètre des racines et de la tige a augmenté de façon marquée après la coupe, mais le fait que la croissance racinaire des semis ait été supérieure suggère, à court terme, qu'une amélioration de l'absorption et du transport des ressources du sol, et probablement de la stabilité, peut être à court terme plus importante qu'une augmentation de la croissance en hauteur et en diamètre de la tige. La réaction des semis était fortement dépendante de leur taille, ce qui semble refléter, pour les individus les plus grands, une plus forte demande des ressources du sol ainsi que de plus fortes intensités lumineuses et une meilleure vigueur des semis avant la coupe. Les rapports de croissance n'ont pu expliquer la réaction plus rapide généralement attribuée aux sapins ou la réaction étonnamment rapide des épinettes. La forte vigueur avant coupe des épinettes, possiblement influencée par le couvert feuillu, pourrait expliquer leur réaction rapide suite à l'ouverture du couvert.

[Traduit par la Rédaction]

Introduction

Deciduous-dominated forests with a conifer understory are a common and widespread feature in the boreal forests of Canada. Tree or tree-group mortality observed in these stands can be mimicked in many ways by partial cuts. However, the use of nonclearcut silvicultural systems that involve releasing understory conifers requires a better understanding of how boreal tree species respond to release.

Partial or complete canopy removal can markedly modify the growing conditions of understory seedlings. From a cool and humid environment, seedlings are suddenly exposed to increased light availability, increased magnitude of temperature fluctuations, and elevated transpirational demand, with the degree of these changes being proportional to canopy removal intensity (Dalton and Messina 1995; Carlson and Groot 1997). Following these changes, trees must make physiological and structural adjustments to reestablish an ap-

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propriate functional equilibrium within the tree. In effect, shade-acclimated seedlings present characteristics that do not promote growth in high-light environments. They have a lower proportion of root mass (Poorter and Nagel 2000) associated with a small amount of conducting tissues (Waring 1987) that have a high resistance to water transport (Sellin 1997, 2001). As a result, trees need to improve soil resource capture and water transport, and this can be done by increasing root surface area and the cross-sectional area of conducting tissues (Vaartaja 1951; Kneeshaw et al. 2002), but sometimes at the expense of height growth (Herring and Etheridge 1976; Tucker et al. 1987). Such a response is in accordance with the optimum-allocation theory, which suggests that trees will modify their allocation pattern to capture the resource that most limits growth (e.g., Poorter and Nagel 2000).

The literature indicates substantial variability in relationships between seedling height before release and growth responses. Some studies have found that growth responses decline with increasing seedling height (Vaartaja 1951; Hatcher 1964; Murphy et al. 1999; Kneeshaw et al. 2002), while others report the opposite pattern after canopy removal (McCaughey and Schmidt 1982; Örlander and Karlsson 2000; Glöde 2002; Comeau et al. 2003). Different factors could explain these conflicting responses. One explanation for the poorer response of taller trees could be that these trees are more suppressed under a given light environment than smaller ones. Suppression level is important since release responses are often closely related to vigour of trees before release (McCaughey and Ferguson 1988; Ruel et al. 2000). Taller seedlings are further disadvantaged following release, since whole-plant respiration increases as size and temperature increase (Waring 1987), thus leaving less carbohydrates available for growth (Ferguson and Adams 1980). On the other hand, the better response of taller individuals could be associated with trees experiencing higher light levels before canopy removal or other advantages related to greater height. Light availability varies in space and time in forests (Lieffers et al. 1999), with light availability increasing with height above ground (Constabel and Lieffers 1996; Messier et al. 1998; Comeau and Heineman 2003). A recent study suggests that a small increase in light availability above critical values may be all that is required to significantly improve the potential responsiveness of taller trees to release (Claveau et al. 2002).

Response of seedlings following canopy removal is also species specific, with shade-tolerant species having a better response and being less affected by length of suppression before release than less shade-tolerant species (Vaartaja 1951; Wright et al. 2000). True firs (*Abies* species) generally show a shorter growth delay following release than spruces (McCaughey and Ferguson 1988) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Helms and Standiford 1985), with spruces showing the slowest response (Carlson and Schmidt 1989). These differences in response coincide mostly with the shade-tolerance ranking of these species — true firs are considered the most shade-tolerant genera among this group, while spruces and Douglas-fir have comparable rankings (Klinka et al. 1990; Sims et al. 1990). However, it is not clear which allocational attributes confer true firs with their ability to better respond to release.

We present results from a study designed to examine above- and below-ground responses of conifer seedlings following different levels of removal of overstory deciduous canopies. More specifically we wanted to answer the following questions: (1) How does allocation to roots, stem, and height change following release? (2) Do above- and below-ground growth vary along a gradient of thinning and pre-release height? (3) Do differences exist among species?

Material and methods

Study sites and experimental layout

This study was conducted in two regions in Canada so that our results could be more easily generalize. Douglas-fir, interior spruce (a complex of white spruce (*Picea glauca* (Moench) Voss) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.)), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) were studied in the Interior Cedar–Hemlock wet cool subzone, Quesnel variant (ICHwk2) (Steen and Coupé 1997) in the interior region of British Columbia. This study site was located at 52°30′N, 121°31′W, at an elevation of 800 m above sea level. Balsam fir (*Abies balsamea* (L.) Mill.) was studied in a stand in northwestern Quebec in the boreal balsam fir – white birch domain, balsam fir – white birch type (5a-T MS26) (Grondin et al. 1999) (48°27′N, 79°26′W). In both regions, selected study sites were on well-drained and fine-textured morainal soils. Yearly mean precipitation and temperature are 842 mm and 4.0 °C in British Columbia (Steen and Coupé 1997), and 857 mm and 0.8 °C in Quebec (Environment Canada 1993).

At each location, overtopping deciduous trees were thinned to different densities to create a gradient of light availability after canopy removal. In British Columbia, the study was established in a 35-year-old stand dominated by white birch (*Betula papyrifera* Marsh.). Before thinning (fall 1996), white birch had an average height of 7.7 m, an average density of 10 700 stems/ha, and an average basal area of 9.4 m^2/ha. Five thinning intensities were replicated three times for a total of 15 plots, using a completely randomized design (Comeau et al. 1999). Because of limited availability in advance regeneration, three plots representing three thinning intensities (clearcut, 800 stems/ha, and control) were selected within one replicate. In Quebec, we chose a 70-year-old trembling aspen (*Populus tremuloides* Michx.) stand with a multicanopied conifer understory. At the time of thinning (spring 1996), the average height of dominant trees was 22 m, the average density was 916 stems/ha, and the stand basal area was 31.1 m^2/ha. Four thinning intensities (0% (control), 25%, 50%, and 100% (clearcut) of the initial deciduous basal area) were replicated once and randomly assigned within one block for a total of four plots.

Tree selection and measurements

In both regions, transects were established at 5 m intervals inside a central 40 m × 40 m subplot. The 262 seedlings in British Columbia and the 119 seedlings in Quebec were sampled along these transects, where seedlings did not undergo direct aboveground competition from neighbouring vegetation and showed no sign of injury, disease, or damage, as to obviate the potential effects of these factors. Three years after thinning, height growth of all sampled trees was

measured retrospectively to cover 8 years of growth (5 years pretreatment and 3 years posttreatment), and tree height at the time of release was estimated. Stem and root disks were collected from 15 trees for each combination of species and treatment in British Columbia and from 23 balsam fir in each treatment in Quebec. A single stem disk was cut immediately above butt swell, and one root disk was removed from the largest lateral root just below the swell of the stump. The second largest root was sampled when the largest root did not clearly dominate. Given the correlation between root diameter and root length or root biomass (Mäkelä 1997; Smith 2001), we assume that the use of the largest root(s) could represent an important proportion of the root system but the exact relationship with other root traits is unknown. During root sampling, only roots that were at least 8 years old and were in the ground were selected to ensure that growth stimulation from light was not involved in root response (Fayle 1968). Once in the laboratory, disks were sanded and ring width was measured for each of the previous 8 years using a micrometer (Velmex Unislide TA, Bloomfield, New York) along each of the four perpendicular radii offset by 22.5° from the largest diameter (Siostrzonek 1958 in Zarnovican 1985). Growth measurements from two root disks were averaged. We assume that stem and root diameter growth are linked to an increase in water-conducting potential, since their conducting potential is correlated with their diameter (Kozlowski and Pallardy 1997). Growth of the largest lateral root(s) was also used to estimate how much growth is being allocated to roots (Kneeshaw et al. 2002). We assume that diameter growth reflects improvement in soil resource uptake. This assumption is based on the relationship between the diameter and the length or the biomass of a root (Mäkelä 1997; Smith 2001), but we do not know the exact relationships between root diameter and other root traits that are more relevant to soil resource uptake (e.g., fine root and root surface areas).

Light measurements

Light availability was measured under cloudy conditions with quantum sensors (Gendron et al. 1998) and with LAI 2000 (LI-COR Biosciences, Lincoln, Nebraska) following thinning in British Columbia when two units became available (Claveau et al. 2002). However, light availability data before and after release were not used in statistical analyses because the significant correlation ($p \leq 0.03$) for most species between light availability and tree height at the time of release would inflate probability values (Underwood 1997) and hence lead to misleading statistical results.

Statistical analyses

Allocation to root, stem, and height growth before and after release was investigated using absolute growth rates, whereas ratios were used for a detailed analysis. The absolute growth rates were examined following model [1] using repeated measures analysis, where the 5-year mean value before thinning was used as the first time step:

$$[1]\quad \text{Growth} = \text{constant} + T + H + T \times H + \varepsilon$$

where T represents thinning treatments, H is tree height at the time of release, and ε is the error term of the model. The model for British Columbia data also included species and all possible interactions involving this term.

Growth ratios used in the detailed analysis allow a finer examination of the allocation patterns than is typically done in comparable studies. These ratios were height/stem growth ratio (height growth / stem diameter growth), height/root growth ratio (height growth / root diameter growth), and stem/root growth ratio (stem diameter growth / root diameter growth). Analyses were also performed using model [1].

For all repeated measures analyses, comparisons from one year to the next were done using planned contrasts (Wilkinson and Coward 1996), whereas differences among growth type, species, or treatments were tested using Tukey's test. For all analyses, data were transformed using square root, base 10 logarithm, or rank when residuals were heteroscedastic or not normal. Results were considered statistically significant at $p \leq 0.05$. Statistical analyses were performed using the GLM procedure of SYSTAT version 10 software package (Systat, Point Richmond, California).

Results

Above- and below-ground responses along thinning and height gradients

Responses were generally proportional to canopy removal intensity but other factors interacted as well, notably tree height and year (Tables S1 and S2[3]) (subsequent presentation of results is justified by significant terms). In British Columbia, root and stem diameter growth increased with thinning intensity, except in the first year following release, when seedlings in the partial-cut treatment had greater growth rates. Height growth in the thinned treatments showed a clear difference from that in the control treatment in the third year only (Fig. 1). Taller individuals grew faster, and the effect of size was stronger with increasing thinning intensity. In Quebec, stem and root diameter growth increased gradually and significantly following release, while taller seedlings grew faster than smaller ones (data not shown). Height growth differed from this pattern, with values decreasing significantly in the first year following release and increasing gradually afterward (Fig. 2).

Examination of the significant terms for growth ratios reveals that these ratios can be split into two groups. For the first group, the stem/root growth ratio shows that roots had a greater response than stems following release and that stem and root growth reached comparable levels in the two following years (Fig. 3). Seedling size was also important in British Columbia, where taller released seedlings allocated more to root diameter growth in the first growing season following release (Fig. 3). Regarding the second group, the height/stem growth and the height/root growth ratios of released trees decreased following thinning, indicating that trees allocated more to root and stem diameter growth than

[3] Supplementary data for this article are available on the journal Web site (http://cjfr.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5033. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

Fig. 1. Growth response of British Columbia species in relation to thinning intensity and seedling height at the time of release. Treatments are control (solid line and circles), 800 stems/ha (broken line and crosses), and clearcut (dotted line and pluses). Periods are first, second, and third growing season following release (1st, 2nd, and 3rd, respectively). Asterisks indicate a significant slope ($p \leq 0.05$). No statistical comparison among treatments could be performed because many interactions terms between treatment and height were significant.

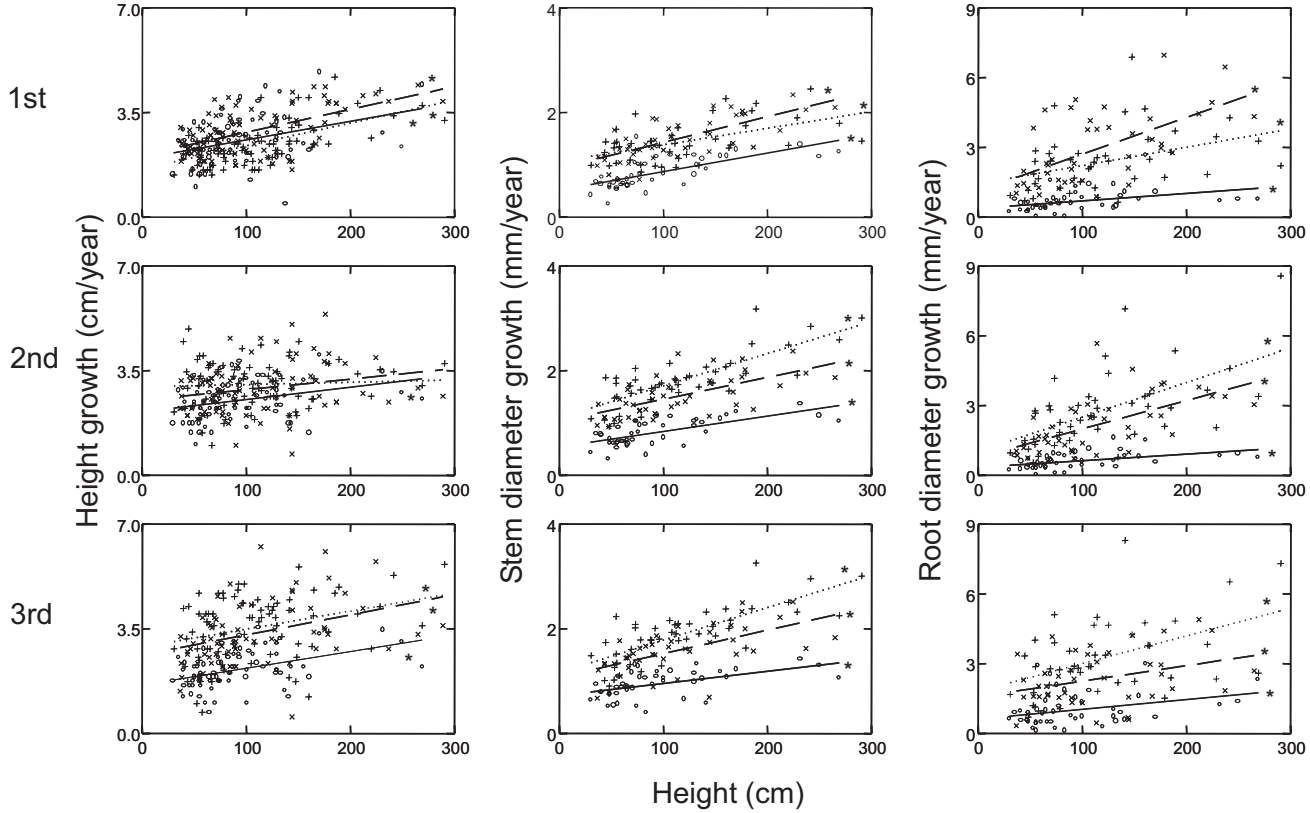
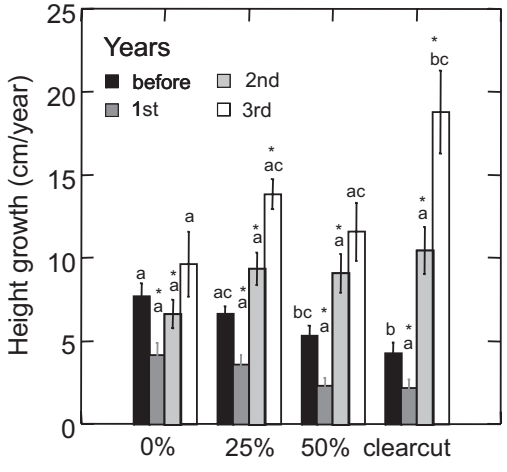


Fig. 2. Influence of time from release on height growth of balsam fir (Quebec) as a function of thinning intensity. Bars with different letters show a significant difference ($p \leq 0.05$) between treatments within a year. Asterisks indicate a significant difference among years within a treatment.



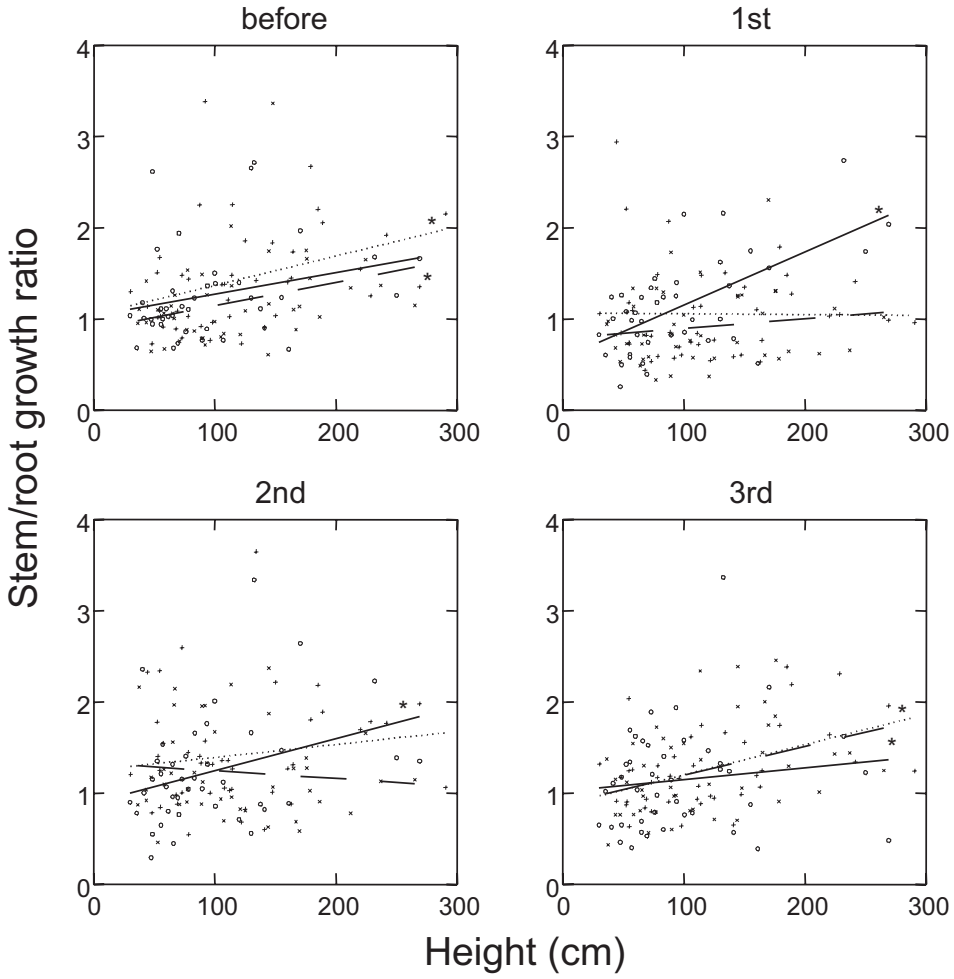
to height growth following release. For Quebec trees, root diameter growth became gradually similar to height growth over time (data not shown), whereas in British Columbia, taller individuals showed a greater allocation to stem and root diameter growth, especially for released trees (Fig. 4).

Differences among species

Species, or its interaction with other factors, also had significant effects, but less so than tree height and treatment. Height growth of British Columbia species showed a complex response to release, with a significant interaction among year, species, treatment, and height. Further examination of this interaction was not possible, since height gradients were very different among combinations of species and treatment. Height gradients must have a comparable range among these combinations to make meaningful statistical analyses (Underwood 1997). These differences in height gradients were not present in simpler interactions, allowing the interpretation of results. Height growth increased with time after release, but species showed contrasting response patterns. Compared with prerelease values, height growth of Douglas-fir and subalpine fir increased in the third year following release, whereas the growth of interior spruce increased from the first year after canopy removal (Fig. 5).

A significant interaction term involving species was found for height/root growth and stem/root growth ratio but trends or patterns among species were observed for height/root growth ratio only. Douglas-fir had a greater height growth per unit of root diameter growth than subalpine fir and inte-

Fig. 3. Periodic variations in stem/root growth ratio in relation to thinning intensity and seedling height at the time of harvest for British Columbia species. Periods are before release (before) and first, second, and third growing season following release (1st, 2nd, and 3rd, respectively). Asterisks indicate a significant slope ($p \leq 0.05$). See Fig. 1 for treatment codes.



rior spruce in the third growing season following release (Fig. 6). Thinning only modified the response of interior spruce: its greater height growth per unit of root diameter growth resulted in the highest height/root growth ratio values in the partial-cut treatment (data not shown).

Discussion

Seedlings can experience severe and complex changes in their growing conditions following canopy removal. Trees that were growing in cool environment with constant humidity conditions are suddenly exposed to a brighter, hotter, and drier environment. Trees must respond to these increases in light and transpirational demand by making physiological and morphological changes to reestablish a functional equilibrium with their new environment and ultimately take advantage of the new growing conditions.

Functional response of seedlings to canopy removal

In the first growing season following release, stem diameter and root diameter growth of British Columbia trees were greater in the partial-cut than in the clear-cut treatment. This pattern, also observed with height growth in Quebec (Fig. 2) and in other studies (Tucker et al. 1987; Koppenaal et al. 1995), can be related to the greater moisture stress experienced by seedlings in the clear-cut treatment (Dalton and Messina 1995). Moisture stress first affects growth of distal parts of trees, and this effect can gradually move down to the roots if soil moisture does not increase. Once soil moisture is replenished, roots are the first organ to resume growth and the distal parts, the last ones (Luxmoore et al. 1995; Taiz and Zeiger 2002). From the second year following release, growth became proportional to thinning intensity, as seedlings had presumably adjusted their root system to the new growing conditions.

Besides thinning intensity, seedling size also influences allocation pattern, as shown by growth ratios. Taller seedlings assigned a higher priority to root diameter growth than to height or stem diameter growth after harvesting. A greater and a faster root diameter growth response has also been observed in other studies following release (Fayle 1975; Kneeshaw et al. 2002; Ruel et al. 2003), and such a response could be attributed to greater transpirational requirements of taller individuals. Woody plants under lower light conditions have a smaller root/shoot ratio (Poorter and Nagel 2000) and a small amount of conducting tissues (Waring 1987) with a

Fig. 4. Periodic variations in (*a*) height/stem growth and (*b*) height/root growth ratios in relation to seedling height before and after release. Periods are before harvest (solid line and circles) and first (large broken line and crosses), second (fine broken line and pluses), and third (dotted line and triangles) growing season following release. All treatments are combined.

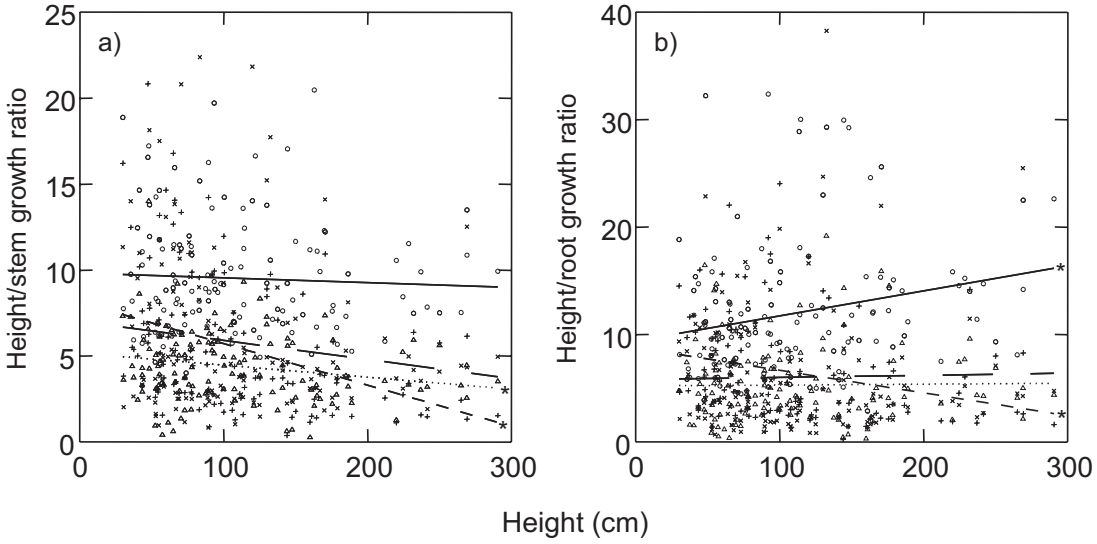


Fig. 5. Periodic variations in height growth of British Columbia species for all treatments combined. Bars with different letters show a significant difference ($p \leq 0.05$) between species within a year. Asterisks indicate a significant difference among years within a species. Periods are the same as those in Fig. 2.

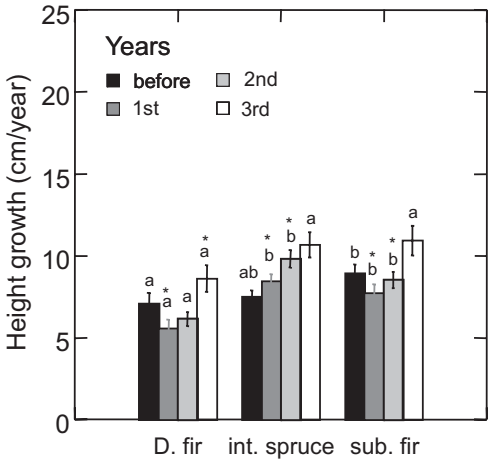
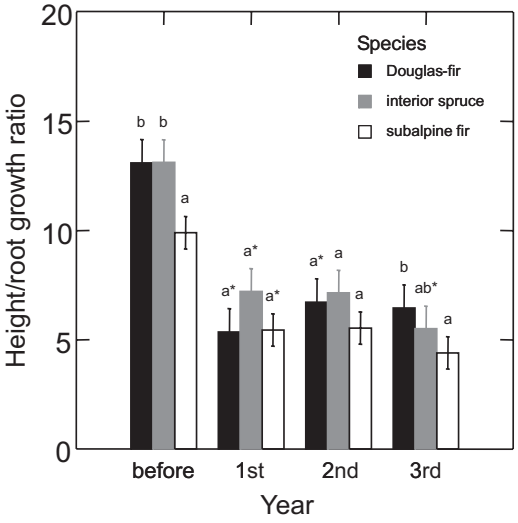


Fig. 6. Periodic variations in height/root growth ratio of British Columbia species. All treatments are combined. Asterisks indicate a significant difference among years within a species. See Fig. 5 for statistical significance codes.



high resistance to water transport (Sellin 1997, 2001). The larger foliage mass of taller individuals could have triggered a greater transpirational demand, and taller seedlings had to increase to a greater extent their ability to capture and transport soil resources to adjust to new growing conditions. Such hypotheses appear reasonable even if relationships among root diameter growth, transportation capabilities, and root traits that are more relevant to soil resource uptake are unknown. Contrary to root and stem diameter growth, all ratios did not differ among thinning intensities, suggesting that this response pattern is not limited to the most demanding growing conditions.

The strong root diameter growth response observed here and the larger root system observed elsewhere following release (Herring and Etheridge 1976; Koppenaal et al. 1995) contrast with conclusions from a metaanalysis on optimum-allocation theory. Poorter and Nagel (2000) concluded that seedlings under moisture stress typically show a modest allocation change to roots. However, contrary to moisture stress trials, partial cutting and clear-cutting can increase soil water availability (Tucker and Emmingham 1977; Bréda et al. 1995). Higher soil moisture availability presumably favoured root diameter growth, as has been observed in other studies under drier conditions (Ladefoged 1939; Krause and Eckstein 1994).

Factors other than moisture stress could also trigger increased root diameter growth following release. The first factor could be related to the support function of roots. Thinning of the canopy trees probably increased wind velocity in the understory, and this could result in increased movement of stems. Since tree growth also responds to me-

chanical stress (Wilson 1975; Morgan and Cannell 1994), studied seedlings could have responded to greater sway by thickening structural roots (Coutts 1983; Nicoll and Ray 1996; Ruel et al. 2003). Although our experiment cannot separate the impact of greater support function on root diameter growth, studies on thinned trees prevented from swaying show a substantial increase in root diameter growth associated with thinning (Wilson 1975).

The second factor associated with greater root diameter growth could be related to the carbohydrate storage function of roots. Following release, trees will tend to increase their production rate, and more carbohydrates might be available for storage, since trees can photosynthesize and transport assimilates down the tree even under severe moisture stress (Luxmoore et al. 1995; Taiz and Zeiger 2002). However, the effects of an increase in root carbohydrates were shown to increase root biomass but not root volume (Landhäusser et al. 2001) and presumably root diameter growth.

Table 1. Percentage of full sunlight for studied seedlings following release.

Treatment	Mean (range)*
British Columbia	
Control	18.9 (6.9–29.3)a
800 stems/ha	61.7 (29.7–74.5)b
Clearcut	92.3 (82.6–99)c
Quebec	
Control	9.5 (4.0–16.0)a
25%†	18.9 (9.5–28.9)b
50%†	21.6 (7.3–42.1)b
Clearcut	38.2 (13.6–65.7)c

*Differences among thinning intensities were tested using one-way ANOVA, where treatments were compared using Tukey's test. In each region, different letters show significant differences ($p \leq 0.05$) between treatments.

†Percentage of hardwood basal area removed.

Differences among species and between regions

Our results concur, in part, with those summarized by McCaughey and Ferguson (1988), which showed that true firs responded rapidly to release. However, based on the allocational attributes studied here, it was not possible to explain the superiority of this genus. According to Wright et al. (2000), shade-tolerant species such as true firs are less affected by length of suppression before release than less shade-tolerant species. Acclimations that reduce the level of suppression before release (e.g., higher allocation to foliage, more efficient light capture, Messier et al. 1999) appear to be important.

The greater tolerance to moisture stress reported for Douglas-fir (Klinka et al. 1990) could constitute an advantage over the other species, as Douglas-fir could better cope with the higher transpirational demand resulting from harvesting. However, the slower response of this mid-shade-tolerant species supports the hypothesis stated above that acclimations that reduce the level of suppression are involved in the faster response to release.

Contrary to other studies (McCaughey and Ferguson 1988; Carlson and Schmidt 1989), we found that interior spruce responded faster than subalpine fir and Douglas-fir and this response could not be attributed to difference in allocations to root, stem, or height growth. This swifter response could be related to the use of the higher light availability when the overstory hardwood trees are leafless in the spring and in the fall. White spruce (Lieffers et al. 1999), Douglas-fir (Bigley 1988), and probably true firs can photosynthesize during these periods, but spruces could take better advantage than other species of these growing conditions. This would decrease their suppression level in the understory and, in turn, improve their response to release.

Trees were studied in two different regions and under different forest conditions to improve the robustness of our results. As observed in other studies (Fayle 1975; Kneeshaw et al. 2002; Ruel et al. 2003), root diameter growth of studied trees showed a stronger response to release than stem diameter growth. Differences diminished over time, suggesting that the trees gradually adjust to new growing conditions. Some differences were also observed between regions. Seedling height at the time of release was more important for understanding the response of seedlings in British Columbia than in Quebec. Kneeshaw et al. (2002) also observed a similar response where root diameter growth did not vary with seedling size. In both cases, the main canopy was partially opened (see Table 1), and this could have lessened the functional difference between smaller and taller individuals.

Forest management implications

Initial tree height can be an important factor in the response of trees to release, since it can determine the immediate light environment of seedlings, their likelihood of being suppressed, and their respiration rate (Waring 1987; Lieffers et al. 1999; Ruel et al. 2000). Contrary to other studies (Vaartaja 1951; Hatcher 1964; Murphy et al. 1999; Kneeshaw et al. 2002; but see Krasowski and Wang 2003), we found that taller individuals had the highest growth rates. The higher light availability with increasing distance from the ground observed here and elsewhere (Constabel and Lieffers 1996; Messier et al. 1998; Comeau and Heineman 2003) may have made the taller trees more vigorous. Claveau et al. (2002) showed that taller trees may have a much better ability to respond to release when receiving more than 10% of full sunlight when shaded. Consequently, tree height should not be a discriminating criterion in postharvest regeneration surveys because only a fraction of the taller seedlings may show a poor response to release. However, taller seedlings must meet other criteria (vigour, absence of disease or wound) to be classified as acceptable regeneration. In addition, susceptibility to windthrow needs to be considered because taller released trees are more prone to such damage (Navratil et al. 1994) and factors improving tree stability might not be met (Ruel 1995; Coutts et al. 1999).

Understory conifer trees growing under overstory deciduous canopies responded rapidly to new growing conditions, and growth was proportional to thinning intensity, as is generally observed in the literature (McCaughey and Schmidt 1982; Oliver and Dolph 1992; Sundkvist 1994; Örlander and Karlsson 2000; Teng et al. 2003; but see Mård 1996; Simard and Hannam 2000). Although seedling growth is important for the long-term productivity of the stand, the selection of a

thinning intensity must also consider other silvicultural and forest management objectives such as total stand yield, the potential for development of competitive vegetation in mixedwood stands (Krasowski and Wang 2003; MacDonald et al. 2004), and the stand structure and composition that are desired for biodiversity conservation purposes (Attiwill 1994; Franklin et al. 1997).

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